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Enduring science: Three decades of observing the Northeast Atlantic from the Porcupine Abyssal Plain Sustained Observatory (PAP-SO)

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ABSTRACT

Until the 1980s, the deep sea was generally considered to be a particularly stable environment, free from major temporal variations (Sanders, 1968). Studies in the abyssal northeast Atlantic by Billett et al. (1983), and subsequently Lampitt (1985) discovered seasonal pulses of surface primary production-derived particulate organic matter (phytodetritus), and hence carbon, at abyssal depths. These early observations were subsequently extended to the central oceanic region of the NE Atlantic (Pfannkuche, 1993; Thiel et al., 1989), and prompted the establishment of more concerted time series studies in the Porcupine Abyssal Plain area. Today, the Porcupine Abyssal Plain Sustained Observatory (PAP–SO) is a multidisciplinary open-ocean time series site in the NE Atlantic (48°50′N 16°30′W, 4850 m water depth; Fig. 1), focused on the study of connections between the surface and deep ocean. *In situ* measurements of climatically and environmentally relevant variables have been made for more than 30 years. This represents an exceptionally long time series - a recent compilation of biological time series data, across terrestrial, freshwater, and marine realms, indicates an average duration of only 13-years (Dornelas et al., 2018). Long-term time series in the deep sea are rare, particularly those collecting data from surface to seabed. The PAP-SO is one of two abyssal long-term time series sites globally (Smith et al. 2015), the other being a thirty-year time series at Station M in the northeastern Pacific Ocean (34°50′N, 123°00′W, ~4000 m water depth), maintained by the Monterey Bay Aquarium Research Institute (Smith et al., 2020). This 'sibling' abyssal time series site also aims to understand the connections between the surface ocean and the seabed, using many similar techniques (Smith et al., 2017), facilitating comparisons between the two sites (e.g. Durden et al., 2019; Durden et al., 2020a; Laguionie-Marchais et al., 2013; Smith et al., 2009). Another source of extended comparison is the 21 year time series Long-Term Ecological Research Observatory HAUSGARTEN, Frontiers in Arctic Marine Monitoring (FRAM) in the Fram Strait between the North Atlantic and the central Arctic Ocean (78.5°N–80°N, 05°W–11°E, 250–5500 m water depth), maintained by the Alfred Wegener Institute for Polar and Marine Research (Soltwedel et al., 2016; Soltwedel et al., 2005). Much of our understanding of temporal variation in the deep sea, and connections between the surface ocean and the seabed have been derived from research conducted at these observatories.

1. Deep-ocean time series

Until the 1980s, the deep sea was generally considered to be a particularly stable environment, free from major temporal variations (Sanders, 1968). Studies in the abyssal northeast Atlantic by Billett et al. (1983), and subsequently Lampitt (1985) discovered seasonal pulses of surface primary production-derived particulate organic matter (phytodetritus), and hence carbon, at abyssal depths. These early observations were subsequently extended to the central oceanic region of the NE Atlantic (Pfannkuche, 1993; Thiel et al., 1989), and prompted the establishment of more concerted time series studies in the Porcupine Abyssal Plain area.

Today, the Porcupine Abyssal Plain Sustained Observatory (PAP–SO) is a multidisciplinary open-ocean time series site in the NE Atlantic (48°50′N 16°30′W, 4850 m water depth; Fig. 1), focused on the study of connections between the surface and deep ocean. *In situ* measurements

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Long-term time series in the deep sea are rare, particularly those collecting data from surface to seabed. The PAP-SO is one of two abyssal long-term time series sites globally, the other being a thirty-year time series at Station M in the northeastern Pacific Ocean (34°50′N, 123°00′W, ~4000 m water depth), maintained by the Monterey Bay Aquarium Research Institute (Smith et al., 2020). This 'sibling' abyssal time series site also aims to understand the connections between the surface ocean and the seabed, using many similar techniques (Smith et al., 2017), facilitating comparisons between the two sites (e.g. Durden et al., 2019; Durden et al., 2020a; Laguionie-Marchais et al., 2013; Smith et al., 2009). Another source of extended comparison is the 21 year time series Long-Term Ecological Research Observatory HAUSGARTEN, Frontiers in Arctic Marine Monitoring (FRAM) in the Fram Strait between the North Atlantic and the central Arctic Ocean (78.5°N–80°N, 05°W–11°E, 250–5500 m water depth), maintained by the Alfred Wegener Institute for Polar and Marine Research (Soltwedel et al., 2016; Soltwedel et al., 2005). Much of our understanding of temporal variation in the deep sea, and connections between the surface ocean and the seabed have been derived from research conducted at these observatories.

2. Development of the observatory

The first operations at the PAP-SO site, in 1985, were largely focused on benthic biology (Thurston, 1986). Over the long-term, core benthic operations have included the collection of megabenthos specimens by epibenthic sledge and/or otter trawl (e.g. Billett et al., 2010; Thurston et al., 1994), and scavenging amphipods by baited trap (e.g. Horton et al., 2020b). Sediment cores have also been collected for meio- and macrobenthos (e.g. Kalogeropoulou et al., 2010; Soto et al., 2010), and various physical and chemical analyses (e.g. Durden et al., 2015a; Durden et al., 2020b). To complement these physical sampling programmes, time-lapse photography of the seabed has been employed to monitor intra- and interannual variation in phytodetritus deposition and benthic activity (e.g. Bett et al., 2001), using the Bathysnap camera lander (Bett, 2003; Lampitt & Burnham, 1983).

The observatory has grown to include meteorological, surface ocean, and mid-water measurements. A time series of sediment traps, typically deployed along with current meters and other oceanographic sensors, has been maintained since 1992 (Lampitt et al., 2010). These sinking particle traps monitor the transfer of organic and inorganic constituents between the surface and the deep ocean. Currently, traps are typically deployed at 3000 m and 4750 m water depth for year-round monitoring, with additional drifting trap operations undertaken during some cruises (Baker et al., 2020). Prior to 2003, water column biogeochemical measurements were made from samples taken on research vessels (Lampitt et al., 2010; Lochte et al., 1993). A near-full ocean depth mooring was operated from 2003 to 2007, recording a suite of biogeochemical parameters from the euphotic zone to the benthic boundary layer. The multidisciplinary set of sensors on the mooring have produced high-resolution *in situ* time series datasets, including subsurface measurements in the deep chlorophyll maximum (30 m depth), which cannot be assessed with satellites. A surface buoy on a full ocean depth mooring was added in 2007, and in 2010 collaboration between the UK Natural Environment Research Council (NERC) and the UK Met Office led to a redesigned infrastructure and the addition of meteorological sensors (Hartman et al., 2012). Recent enhancements to the variables measured in the surface mixed layer include oxygen concentration, solar irradiance, and the carbonate system. These surface ocean biogeochemical, physical and meteorological data are telemetred to the National Oceanography Centre (NOC), UK. The real-time data are available as open access (noc.ac.uk/pap) and in delayed mode, as quality-controlled datasets from the British Oceanographic Data Centre (bodc.ac.uk). In addition, these data are uploaded daily to the European Union's Earth Observation Programme (marine.copernicus.eu) and to the United Nations World Meteorological Organisation's Global Telecommunication System.

When the PAP-SO was established, it was located at a point linking the programmes at the UK's Porcupine Seabight, and the German

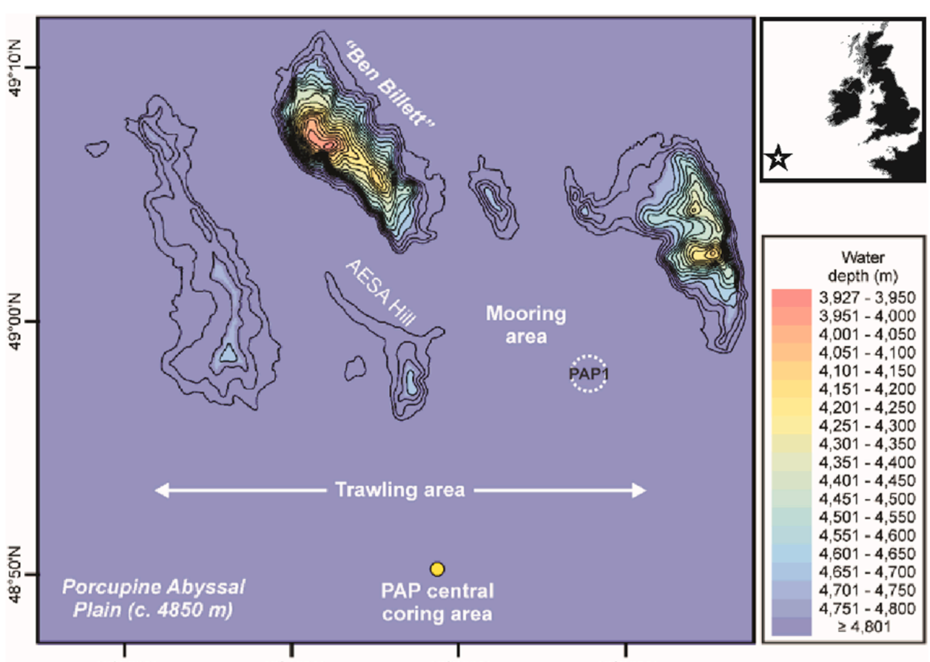

Fig. 1. Location of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) in the northeast Atlantic Ocean showing the typical working areas at the PAP-SO for a range of operations (demersal trawling, seabed coring, seabed moorings) and the current location of the "PAP1" surface buoy. Bathymetry based on composite multibeam echosounder data (Lampitt, 2010; Ruhl, 2012) illustrated at 50 m-intervals. [WGS84, Mercator projection]

BIOTRANS site (Biologischer Vertikaltrasport und Energiehaushalt in der bodennahen Wasserschicht der Tiefsee; see e.g. Thiel et al., 1989). European collaboration at the site was expanded through several projects funded from the European Union (e.g. Billett & Rice, 2001; Rice et al., 1994). The PAP-SO continues to be part of European and international networks, such as the international 'OceanSITES' project, European networks such as EMSO (European Multidisciplinary Seabed Observatory; Best et al., 2016), and ICOS (Integrated Carbon Observing System), and EU projects such as EuroSITES FP7 Collaborative Project (2008–2011), FixO3 (Fixed point Open Ocean Observatory, 2013–2017), and iFADO (Innovation in the Framework of the Atlantic Deep Ocean, 2017–2021). It is also a core site within the UK National Capability programme and has had contributions from NERC 'Oceans2025', and the Climate Linked Atlantic Sector Science funding. These collaborations have greatly increased the quality and quantity of research outputs from the PAP-SO.

3. Recent research outputs

Major research findings at the PAP-SO in its first ~20 years of operation include the discovery of seasonal input of detritus to the seabed (Billett et al., 1983), revisions to the midwater carbon budget (Giering et al., 2014), and links between interannual detrital supply and benthic community structure (Billett et al., 2010; Billett et al., 2001). The observatory has been the focus for two previous special issues (Billett & Rice, 2001; Lampitt et al., 2010), with elements of the benthic programme having been introduced in an earlier publication (Rice et al., 1994). Content in this new special issue adds 10+ years to the previously published data span, and provides new insights into the pelagic and benthic realms at the PAP-SO. At the start of the United Nations Decade of Ocean Science for Sustainable Development (2021–2030) (Intergovernmental Oceanographic Commission, 2018), which has the development of a comprehensive ocean observing system as one of its priority research and development goals, we believe this special issue is particularly timely. The collected works serve to highlight several of the unique strengths of the PAP-SO, including (a) coverage from the air-sea interface, through the full depth of the water column, to the abyssal seafloor; (b) addressing multiple Essential Climate Variables (Bojinski et al., 2014), Essential Ocean Variables (e.g. Miloslavich et al., 2018), ecosystem Essential Ocean Variables (e.g. Constable et al., 2016), and Essential Biodiversity Variables (e.g. Kissling et al., 2018); (c) serving as a testbed for new and emerging essential variables, sensors, and platforms; and (d) multi-national and multi-agency operation that promotes data banking, sharing, and reuse. As far as possible all data comply with the FAIR principles in being Findable, Accessible, Interoperable, and Reusable (Tanhua et al., 2019).

3.1. The surface ocean

Real-time water column measurements have been made at the PAP-SO site for the last 15+ years using autonomous samplers and sensors (e.g. Hartman et al., 2015; Hartman et al., 2012; Körtzinger et al., 2008). Since the last PAP-SO special issue (Lampitt et al., 2010), there have been many technical enhancements to water column parameter measurement, not least the addition of surface ocean CO_2 and pH measurements. These observations are further supported by data obtained from ships of opportunity (Macovei et al., 2020), gliders (Bol et al., 2018; Damerell et al., 2016; Evans et al., 2018; Hemsley et al., 2015; Rumyantseva et al., 2019), Argo floats, XBTs, and other moored instrument measurements, with some studies combining data from several platforms (Rumyantseva et al., 2015). This work also benefits from the simultaneous provision of meteorological data through a partnership with the UK Met Office.

3.2. Particle flux and the biological carbon pump

The transfer of carbon to the ocean interior, and ultimately to the seafloor, remains a central theme of the PAP-SO science programme (Sanders et al., 2014). The time series of carbon flux measurements has developed over the last 30 years and now includes the use of a variety of techniques (Baker et al., 2020; Le Moigne et al., 2013b), with data incorporated into basin and global-scale compilations (Le Moigne et al., 2013a; Torres Valdés et al., 2014). The biological carbon pump has been extensively studied at the observatory (Frigstad et al., 2015; Giering et al., 2014; Marsay et al., 2015), including the processes driving variability in particle flux (Belcher et al., 2016; Bol et al., 2018; Le Moigne et al., 2014; Riley et al., 2012; Villa-Alfageme et al., 2014), such as variations in zooplankton abundance/community, fatty acids as components of nutrient cycling (Gašparović et al., 2018a; Gašparović et al., 2017; Gašparović et al., 2018b), particle composition (Baker et al., 2017; Belcher et al., 2016), and phytoplankton community structure (Henson et al., 2012). The effects of such surface and midwater processes on fluxes at the seabed and benthic communities have also been examined (Durden et al., 2020a; Horton et al., 2020b; Turnewitsch et al., 2017).

3.3. Seafloor ecosystems

The collection of biological specimens is a cornerstone of benthic research at the PAP-SO. These specimens continue to be collected and curated in the *Discovery Collections* at the National Oceanography Centre (*DISCOLL, NOC, UK;* http://grscicoll.org/institution/national-oceanography-centre-southampton), which serve as an ecological and taxonomic data archive available to other users. Earlier taxonomic discoveries, including descriptions of sea anemones (Riemann-Zürneck, 1991; Riemann-Zürneck, 1997) and octopuses (Collins, 2003), continue to be augmented by new species descriptions and revisions of amphipods, sea cucumbers, and sea pens (Corrigan et al., 2014; Gubili et al., 2017; Horton & Thurston, 2014; Horton & Thurston, 2015; López-González & Williams, 2011). The collected material has enabled detailed studies of the morphology, population structure, and life history of many taxa, including hydroids, amphipods, sea cucumbers, polychaetes, and forams (Cantero & Horton, 2017; Duffy et al., 2016; Kazanidis et al., 2014; Laguionie-Marchais et al., 2013; Stefanoudis et al., 2017; Stefanoudis & Gooday, 2015; Stefanoudis & Gooday, 2016). Rate processes and ecosystem function have also been investigated (Hughes et al., 2011; Ruhl et al., 2014). Since the first operations at the PAP-SO site included the first successful deployment of a free-fall experimental amphipod trap system to collect specimens (Thurston, 1986), it is fitting that this special issue reports the on-going amphipod trap time series studies (Horton et al., 2020b), and provides an update on the taxonomic identities of the Eurythenes species present (Horton et al., 2020a).

In the last decade, seafloor research has expanded from the abyssal plain to include adjacent abyssal hills (Fig. 1) that supply organic matter to the seafloor, and consequently the resident benthic assemblages (Durden et al., 2015a; Durden et al., 2017; Milligan et al., 2016; Morris et al., 2016; Stefanoudis et al., 2016a; Stefanoudis et al., 2016b). This has been enabled by the development and use of mass photography in the quantification of the seafloor environment and fauna (Durden et al., 2016a; Durden et al., 2015a; Durden et al., 2016b; Durden et al., 2016c; Milligan et al., 2016; Morris et al., 2016). These seabed photographs are being used to train artificial intelligence systems (e.g. Durden et al., in review; Zurowietz et al., 2018) that will improve the quality and speed at which important data products can be assembled, to ensure that data processing can keep pace with the increased data rate from new sensors and platforms. In addition, time-lapse photography at the observatory continues to play a significant role in assessing organism behaviour (Durden et al., 2015b), and the processing and transformation of organic matter at the seafloor (Durden et al., 2019; Durden et al., 2020a; Durden et al., 2017). These photographic techniques continue to be developed and provide further insights into the benthic ecology of the observatory site.

4. Contributions in this special issue

This special issue celebrates the breadth of studies at the PAP-SO over the last 30 years and includes 15 papers presenting studies from the surface to the abyss.

1. *The productive northeast Atlantic* - The development of spring blooms in the northeast Atlantic were tracked using gliders near the PAP-SO over a full year. This unique dataset showed that the region is autotrophic over an annual cycle and that the water is oxygen undersaturated during the whole winter period. Using the oxygen data to calculate productivity showed that net community production is relatively high at the PAP-SO compared with previous estimates. Productivity peaks at different times of the year were examined and were shown to have different drivers (Binetti et al., 2020).
2. *The influence of weather on productivity*- A unique 8-month glider dataset was used to investigate phytoplankton bloom initiation and three hypotheses for the mechanism of spring bloom initiation were examined. Results were consistent with the critical depth hypothesis when mixing depth is considered. Bloom initiation in this region of the northeast Atlantic is prompted by favourable light and mixing depth conditions. Periods of high winds and increased convective mixing appear to delay the spring blooms (Rumyantseva et al., 2019).
3. *Physical and biological process and carbonate chemistry* - The productive PAP-SO region is significant as a carbon sink, with measurements now available from the observatory itself and from a ship of opportunity that passes each month. The annual mean seawater pCO_2 has not increased between 2002 and 2016 at the PAP-SO, however the winter-summer seasonality of seawater pCO_2 has increased with time. The study area is a carbon sink with increasing CO_2 flux into the ocean. Gas exchange, biological production and mixing explain most of the pCO_2 variability with about 77% of the annual change in pCO_2 influenced by productivity and temperature (Macovei et al., 2020).
4. *Influence of physical mixing, using satellite and altimetry data* - An observationally based estimate for the upper 1000-m transport of the North Atlantic Current (NAC) between the Porcupine Abyssal Plain (PAP) and the Central Irminger Sea (CIS). This study extends the NAC time series back in time to the pre-Argo period using a combination of floats, altimetry, moorings, and XBT data. It links decadal variability to sea level anomalies and density signals, quantifies errors and confirms that the signals are indeed larger than the uncertainty estimates (Lankhorst & Send, 2020).
5. *Mixing investigated using models and data* - A comparison of 5 mixed layer depth (MLD) models and *in situ* data from gliders suggest that the models reproduce temperature but may overestimate the mixed layer depth, with average biases between 160 and 228 m. After spring restratification, biases in MLD are small and unrelated to winter biases. Wind influences mixing more in the spring than the autumn, where heat flux appears to be more important, especially in the models (Damerell et al., 2020).
6. *Methods to estimate sinking organic carbon* - Carbon flux estimates from Thorium-based and optical measurement provide fundamental measurements of the flux of carbon through the water column to the mesopelagic. The first inter-comparison of two autonomous, upper-ocean Lagrangian sediment traps reveal that cylindrical sediment traps collect greater particle flux than conical traps (which may in turn under-collect small particles). In summary the magnitude of particle flux and size spectra varied between different types of sampling platform, but they were ultimately more sensitive to the chemical composition of the flux (Baker et al., 2020).
7. *Zooplankton community structure* - To estimate marine snow consumption by small aggregate-feeding copepods at the PAP-SO the biomass and vertical distribution of the harpacticoid *Microsetella norvegica* and the poecilostomatoid *Oncaea* spp. were followed. This was combined with estimates of respiration rates, and various method were also used to estimate feeding rates. The study found that small zooplankton can have a large influence on vertical flux (Koski et al., 2020).
8. *In situ settling dynamics of organic aggregates, from novel techniques* – Size and settling dynamics of marine snow in the mesopelagic was followed using a new optical device. Despite similar optical appearance, similar sized aggregates had different sinking velocities and there was no size-to-settling relationship for the heterogeneously composed aggregates observed down to ~500 m. These results show that it is not only size that impacts aggregate settling and it is important to consider aggregate composition when estimating particle flux from vertical size-distributions (Iversen & Lampitt, 2020).
9. *Abyssal time series of scavenging amphipods* - Long-term observations of near-bottom scavenging amphipod populations at the PAP-SO represents our longest time-span study of the benthos at the PAP-SO to date (1985–2016), and remains an active component of our research to the present day. These results indicate that the taxon composition of scavenging amphipods has changed through time, with a remarkable change in the dominant species since 2011, and that that change might equate to a ‘regime shift’ potentially linked to upper ocean climate as assessed by the Atlantic Multi-decadal Oscillation index. There is also some indication that scavenging amphipod diversity is reduced at times of higher organic matter flux through the deep water column at the PAP-SO (Horton et al., 2020b).
10. *The amphipod genus* Eurythenes *at the PAP-SO* - Detailed studies revealed a species new to science. The giant amphipod genus Eurythenes was previously thought to be represented at the PAP-SO by two cosmopolitan and widely recorded species: *Eurythenes gryllus* and the pelagic *Eurythenes obesus*. Samples of Eurythenes spp. collected using free-fall baited traps were studied using both morphological and phylogenetic analyses. This revealed that there are four distinct species occurring at PAP, one of which is new to science. Three species: *E. maldoror*, *E.* c.f. *magellanicus* and the new species are found in the baited trap samples and *Eurythenes gryllus* has not yet been recorded at the Porcupine Abyssal Plain, although confirmation of this will require further study of the full collection of >5000 Eurythenes specimens (Horton et al., 2020a)
11. *Subtle terrain variation linked to substantive ecological change in the abyssal benthos* - The expansion of observations of megafauna (>1 cm) on the seabed from the abyssal plain at the PAP-SO to include the modest adjacent abyssal hill previously showed a change in the supply of organic matter, sediment particle size, and benthic assemblages (Durden et al., 2015a; Morris et al., 2016). Even very subtle bathymetric variations (~10 m) induce significant changes in benthic megafaunal abundance, diversity, and community structure assessed through autonomous underwater vehicle photographic surveys. Likewise, megabenthic communities in two areas of the abyssal plain differed, despite similar sedimentary characteristics and only a 2 m difference in water depth; this

difference is likely driven by catastrophic disturbance caused by mass wasting from the adjacent seamount (Durden et al., 2020b).

12. *Interspecific and intraspecific associations of benthic megafauna* - The spatial distribution of benthic megafauna in seabed images were used to assess intra, and interspecific associations in three contrasting abyssal habitats. Most organisms were found to have non-random interspecific distributions. Intraspecific networks on the abyssal plain were highly connected, while the network on an abyssal hill had few connections and was highly dependent on a single organism; the difference suggests the operation of different regimes across the habitats and potential vulnerability of the community on the hill to disturbance (Mitchell et al., 2020).
13. *A comparison of methods to quantify megabenthos biomass* - Biomass is a key variable for estimating stocks and carbon flows. A new method of individual specimen biomass estimation from seabed photographs is developed and tested, based on fresh trawl caught material from PAP-SO (Benoist et al., 2019).
14. *Deep-sea sponge aggregations in the Porcupine Seabight* - Prior institutional efforts focussed on the adjacent Porcupine Seabight, included the discovery and description of *Pheronema carpenteri* aggregations (Rice et al., 1990), that are now regarded as "vulnerable marine ecosystems" of particular conservation importance (e.g. Auster et al., 2011). As part of a PAP-SO research cruise (Ruhl, 2012), we revisited the key sites and were able to document apparent substantial degradation of these deep-sea sponge aggregations. By inference, this appears to have been the result of a major expansion in commercial, deep-water demersal trawling in the intervening years (Vieira et al., 2020).
15. *An evaluation of the impact of variations in input data to artificial intelligence-based methods of seabed image analysis* - Artificial intelligence methods are in development to assist with the identification of fauna in seabed photographs, but most studies split their data 80/20 for training and validating a newly-developed model without regard for how the data quantities may alter their results. Using expert-annotated seabed photographs from the PAP-SO, effects of different sizes of training and validation data on the success of a machine-learning algorithm in identifying benthic megafauna are evaluated, along with alterations in the ecological conclusions. The results provide indications of how other developers could select data to appropriately train and validate their models (Durden et al., in review).

5. Closing

These contributions add to the scientific advances at PAP-SO, enhancing our understanding of the links between the surface ocean, midwater, and seabed. Quantifying the temporal variations in the physical, chemical, and biological aspects of these environments, and understanding how they are linked is important to establishing a baseline. This baseline is an important contribution to efforts to observe the ocean globally (e.g. Levin et al., 2019), and also a premise from which we can evaluate and manage changes to the environment. Current and possible anthropogenic changes to the water column and deep seabed include impacts from climate change (e.g. Jones et al., 2014), deep-sea mining (Jones et al., 2017; Washburn et al., 2019), oil and gas development (Jones et al., 2007), and pollution (Pabortsava & Lampitt, 2020; Woodall et al., 2014).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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